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ISBN 83-900337-5-5

ISSN 0065-1710

Okładka – Cover: Jerzy ŚWIECIMSKI

Druk i oprawa: Drukarnia Kolejowa, Kraków

zam. 1401/92, nakł. 800 egz.

Druk ukończono 15 listopada 1992.

Early Pleistocene *Predicrostonyx* (Rodentia, Mammalia) from Poland

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Received: 15 June 1992

Accepted for publication: 30 June 1992

NADACHOWSKI A. 1992. Early Pleistocene *Predicrostonyx* (Rodentia, Mammalia) from Poland. Acta zool. cracov. 35(2): 203-216.

Abstract. A description is given of *Predicrostonyx compitalis* from the locality of Zalesiaki 1A/13. On the basis of the common occurrence of two species of the evolved *Allophaiomys* [*Microtus* (*Allophaiomys*) *pliocenicus praehintoni* and *Microtus* (*Allophaiomys*) *nutiensis*] and the first true *Microtus* species identified here as *Microtus* (*Microtus*) sp. and *Microtus* (*Microtus*) ex. gr. *hyperboreus*, the assemblage is believed to come from above the Lower/Upper Biharian boundary most probably corresponding to the final part of the Matuyama Chron, preceding the Jaramillo event. The early history of *Dicrostonychini* in the Northern Hemisphere is also discussed.

Key words: *Predicrostonyx*, Rodentia, Early Pleistocene, biostratigraphy, Poland.

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I. INTRODUCTION

Collared lemmings (*Dicrostonychini* KRETZOI, 1955) form a well defined group of microtine rodents with characteristic dental traits and thus easily recognizable in the fossil record. At present they show a circumpolar distribution in the Arctic zone of Eurasia and North America (CORBET, HILL 1991) and exhibit remarkable adaptations to the tundra environment (BANFIELD 1974). Many authors used the presence of *Dicrostonyx* in Pleistocene localities as an indicator of a strict tundra plant community in palaeoenvironmental reconstructions. However, during the Late Pleistocene collared lemmings occurred in assemblages of disharmonious faunas, so termed by LUNDELIUS et al. (1983), HORÁČEK, SÁNCHEZ MARCO (1984), GRAHAM (1985), and NADACHOWSKI (1989a) containing tundra and steppe elements which at present show disjunct distribution patterns. These faunal assemblages lived in a particular mosaic plant community (MEAD, MEAD 1988) which has no modern counterpart (YOUNG 1982). The Middle and Early Pleistocene

lemmings therefore may be indicative only of a boreal-type environment, and not necessarily of a recent-type tundra community (KOWALSKI 1980).

The latest fossil records indicate that *Dicrostonychini* evolved in Beringia, which appeared to be one of the most important areas of the evolution of the Pleistocene plant and animal communities (HOPKINS et al. 1982; SHER 1987). In the vast territory ranging from Northeastern Siberia through Alaska to Northern Yukon the history of lemmings including various stages of their evolution is relatively well documented. In Europe *Dicrostonyx* is a dominant element in many Late Pleistocene faunal assemblages. However, the Middle and especially the Early Pleistocene collared lemming remains are recovered only occasionally (FEJFAR 1965, 1966; HELLER, BRUNACKER 1966; BOURDIER et al. 1969; CHALINE 1972; KOWALSKI 1977; FEJFAR, HORÁČEK 1983). It is assumed that the Early /Middle Pleistocene boundary corresponds to the first appearance of *Arvicola* as defined by FEJFAR (1976), HORÁČEK (1981) and FEJFAR and HEINRICH (1983). Accordingly, only the faunistic assemblages from Europe and West Siberia containing both *Mimomys savini* and *Dicrostonychini* were taken into consideration in the present paper.

Since the fossil records of Early Pleistocene lemmings may be of significance for the reconstruction of palaeoenvironment, migration and evolution of *Dicrostonychini*, a description of *Predicrostonyx* from Poland seems expedient.

II. DESCRIPTION OF LOCALITY AND FAUNA WITH *PREDICROSTONYX*

Remnants of a primitive collared lemming have been recovered from the Zalesiaki 1A/13 faunal assemblage (NADACHOWSKI 1990a). The locality of Zalesiaki 1 near Działoszyn, Cracow-Wieluń Upland, discovered in 1970 and now completely destroyed (NADACHOWSKI et al. 1989), yielded 15 faunistic samples. MŁYNARSKI (1977) divided them into two groups: A (samples No 1, 2, 5, 7, 8, 9, 10 and 13) and B (samples No 3, 4, 6, 11, 12, 14 and 15), according to their species composition.

Faunistic information concerning the rodent fauna was first published without detailed differentiation into samples (BLACK, KOWALSKI 1974; KOWALSKI 1977, 1979; PRADEL 1988).

The Zalesiaki 1A fauna contains Biharian micromammals, although particular samples probably differ slightly in age (NADACHOWSKI 1990a, Table III). The following taxa of rodents were recognized in the Zalesiaki 1A/13 assemblage (numbers indicate the frequency of first lower molars – M_1 , if M_1 was lacking, the numeral 1 was inscribed):

Sciuridae

<i>Spermophilus polonicus</i> (GROMOV, 1965)	3	(2.8%)
<i>Pliopeteurista meini</i> (BLACK et KOWALSKI, 1974) ¹	?	

¹the frequency of *P. meini* is unknown, because material from particular samples was not separated

Cricetidae

<i>Cricetus runtonensis</i> (NEWTON, 1909)	5	(4.7%)
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Spalacidae

<i>Prospalax</i> sp.	1	(0.9%)
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Arvicolidae

<i>Predicrostonyx compitalis</i> ZAZHIGIN, 1976	1	(0.9%)
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<i>Lemmus</i> sp.	5	(4.7%)
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<i>Clethrionomys</i> sp.	3	(2.8%)
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<i>Pliomys episcopalis</i> MEHELY, 1914	14	(14.1%)
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<i>Microtus</i> (<i>Allophaiomys</i>) <i>pliocaenicus praehintoni</i> RABEDER, 1981	18	(17.1%)
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<i>Microtus</i> (<i>Allophaiomys</i>) <i>nutiensis</i> CHALINE, 1972 ²	24	(22.8%)
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<i>Microtus</i> (<i>Microtus</i>) ex gr. <i>hyperboreus</i>	6	(5.5%)
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<i>Microtus</i> (<i>Microtus</i>) sp. ³	15	(14.7%)
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<i>Mimomys pusillus</i> (MEHELY, 1914)	4	(3.8%)
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<i>Mimomys savini</i> HINTON, 1910	3	(2.8%)
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Muridae

<i>Apodemus</i> cf. <i>flavicollis</i> (MELCHIOR, 1834)	3	(2.8%)
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Total	106	(100%)
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III. SYSTEMATICS AND MORPHOLOGY

Of the rodents known from the Zalesiaki 1A/13 fauna, the collared lemming and voles (*Microtus*), which are important index fossils, are described here; other species will be presented elsewhere. VAN DER MEULEN's (1973) nomenclature of morphological tooth patterns and measurement methods were used in the description of material.

Dicrostonychini KREZOI, 1955*Predicrostonyx* GUTHRIE et MATTHEWS, 1971*Predicrostonyx compitalis* ZAZHIGIN, 1976

Predicrostonyx sp. – NADACHOWSKI 1989b: 169, Tab. III.

Predicrostonyx cf. *compitalis* – NADACHOWSKI 1990a: 221, Tables 1 and 3.

²including *Microtus* (*Allophaiomys*) *pliocaenicus pliocaenicus* sensu NADACHOWSKI (1990a)

³= *Microtus* (*Microtus*) *nivaloides* sensu NADACHOWSKI (1990a)

Predicrostonyx cf. *compitalis* – NADACHOWSKI 1990b: 240, Tab. 3

Material: left M_1 , fragment of right M^2 , 2 left M^3

Measurements: length of M_1 – 2.95, A/L index – 52.9; length of M^2 – about 1.72; length of M^3 – 2.28 and 1.78

Description: Molars without cement in the re-entrant angles, enamel-free areas present on top of all triangles, thickness of enamel relatively poorly differentiated. M_1 with five closed triangles (Fig. 1/1), anterior cap elongated, LRA5 and BRA4 poorly developed; M^2 possesses an anterior loop and three triangles with a small labial bud (broken) on the last of them (Fig. 1/2); M^3 characterized by the presence of anterior loop and three (Fig. 1/3) or two (Fig. 1/4) triangles as well as a posterior cap with incipient development of BSA4 and LSA5.

Remarks and discussion: The molars show a very primitive pattern. The first lower molar (M_1) (Fig. 1/1) is similar to the holotype of *Predicrostonyx antiquitatis* (CHALINE, 1972) from Les Valerots, which also has five closed triangles (CHALINE 1972, Fig. 66/2), while the type specimen of *Predicrostonyx compitalis* ZAZHIGIN, 1976 is much more complicated and possesses seven closed triangles (ZAZHIGIN 1976, Fig. 1/9). However, the *Predicrostonyx* – *Dicrostonyx* lineage is characterized by a very wide morphological variation of M_1 and in cases when sufficiently big material is available, specimens with five, six and seven triangles can be seen in samples (GUTHRIE, MATTHEWS 1971; NADACHOWSKI 1982; SMIRNOV et al. 1986).

Upper molars of *Dicrostonychini* are much more important to species determination (AGADZHANIAN 1976). The second upper molar (M^2) from Zalesiaki 1A/13 possesses only three triangles and a small bud in the posterior part of the tooth (Fig. 1/2), which can be also observed in *P. compitalis* (ZAZHIGIN 1976, Fig. 1/1) and in some specimens of *Dicrostonyx meridionalis* SMIRNOV et BORODIN, 1986 from West Siberia (SMIRNOV et al.

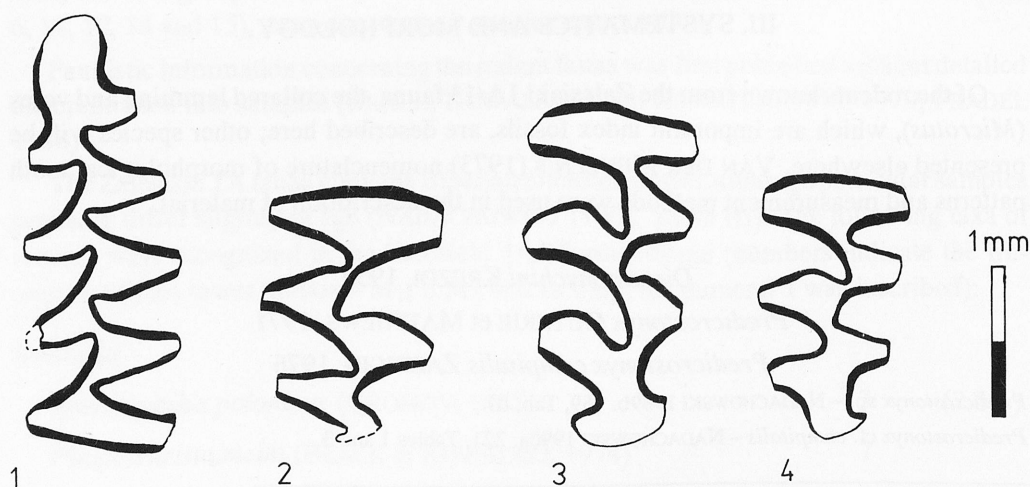


Fig. 1. *Predicrostonyx compitalis*: 1 – left M_1 , 2 – right M^2 , 3 – left M^3 , 4 – left M^3 .

1986, Fig. 15/10-16). In *Predicrostonyx hopkinsi* this molar is characterized by the lack of a labial and/or lingual bud on the last triangle (GUTHRIE, MATTHEWS 1971, Fig. 5/2, 5), while in *Dicrostonyx simplicior* FEJFAR, 1966 and *Dicrostonyx renidens* ZAZHIGIN, 1976 this molar is already more complicated in comparison with the specimen from Zalesiaki 1A/13 (FEJFAR 1966, Fig. 1/b; KOWALSKI 1977, Fig. 5/12; ZAZHIGIN 1976, Fig. 1/3, 5, 6).

Both third upper molars (Fig. 1/3, 4) are similar to the corresponding teeth of *Predicrostonyx hopkinsi*, *P. compitalis* and *Dicrostonyx meridionalis*, which possess two or three closed triangles and a posterior extension, penetrated by poorly developed BRA3 and LRA4 (GUTHRIE, MATTHEWS 1971, Fig. 5/3, 6, 7; ZAZHIGIN 1976, Fig. 1/1; SMIRNOV et al. 1986, Fig. 15/17-20). The pattern of the M^3 occlusal surface in *Dicrostonyx simplicior* and *D. renidens* is much more complicated (FEJFAR 1966, Fig. 1/a, d, e, f; KOWALSKI 1977, Fig. 5/13-15; ZAZHIGIN 1976, Fig. 1/4). A fragment of M^3 from Včeláre 4D/8 assigned by FEJFAR and HORÁČEK (1983) to "*Dicrostonyx* cf. *antiquitatis*" exhibits a complex morphology and should rather be included in the true *Dicrostonyx* (? *simplicior*).

Microtus (Allophaiomys) pliocaenicus praehintoni RABEDER, 1981

Microtus (Allophaiomys) praehintoni sp. nov. – RABEDER 1981: 213-214, Tab. 33, Abb. 135.

Microtus (Allophaiomys) pliocaenicus praehintoni – NADACHOWSKI 1990a: 221, Tab. 3.

Material: 9 complete and 9 damaged M_1 , probably 10 M^3 .

Measurements: length of M_1 – 2.65 - 3.04 (2.83), $N = 9$, A/L index – 40.3 - 47.1 (44.5), $N = 9$

Morphotypes: "praehintoni" – 14 M_1 ; "pitymyoides" – 4 M_1

Description: First lower molars possess three closed triangles, T5 and T6 are confluent; in most of the specimens a distinct development of LRA5 is observed (morphotype "praehintoni", Fig. 2/1-3) as well as the confluence of T5 and T6; few specimens exhibit separation of T5 and T6 (morphotype "pitymyoides", Fig. 2/4); the third upper molar is of medium size with two or three closed triangles (Fig. 2/5).

Remarks and discussion: The remnants of *Microtus (Allophaiomys)* from Zalesiaki 1A/13 belong probably to two species. The larger species exhibits traits characteristic evolved populations of *M. (Allophaiomys) pliocaenicus* and is related to the sample from Deutsch-Altenburg 4B (RABEDER 1981) with addition of some specimens of the "pitymyoides" morphotype which are absent in the type population of "*Allophaiomys praehintoni*". In general, the differences from typical *M. (A.) pliocaenicus* are sufficient to include the population studied in a separate subspecies.

Microtus (Allophaiomys) nutiensis (CHALINE, 1972)

Allophaiomys pliocaenicus nutiensis nov. ssp. CHALINE 1972: 95-99, Fig 24.

Microtus (Allophaiomys) sp. A – VAN DER MEULEN 1973: 60-65, 97-98, Fig. 23-28, Tab. VII, Fig. 1-18.

Microtus (Allophaiomys) nutiensis – NADACHOWSKI 1990a: 221, Tab. 3.

Microtus (Allophaiomys) pliocaenicus pliocaenicus – NADACHOWSKI 1990a: Tab. 3.

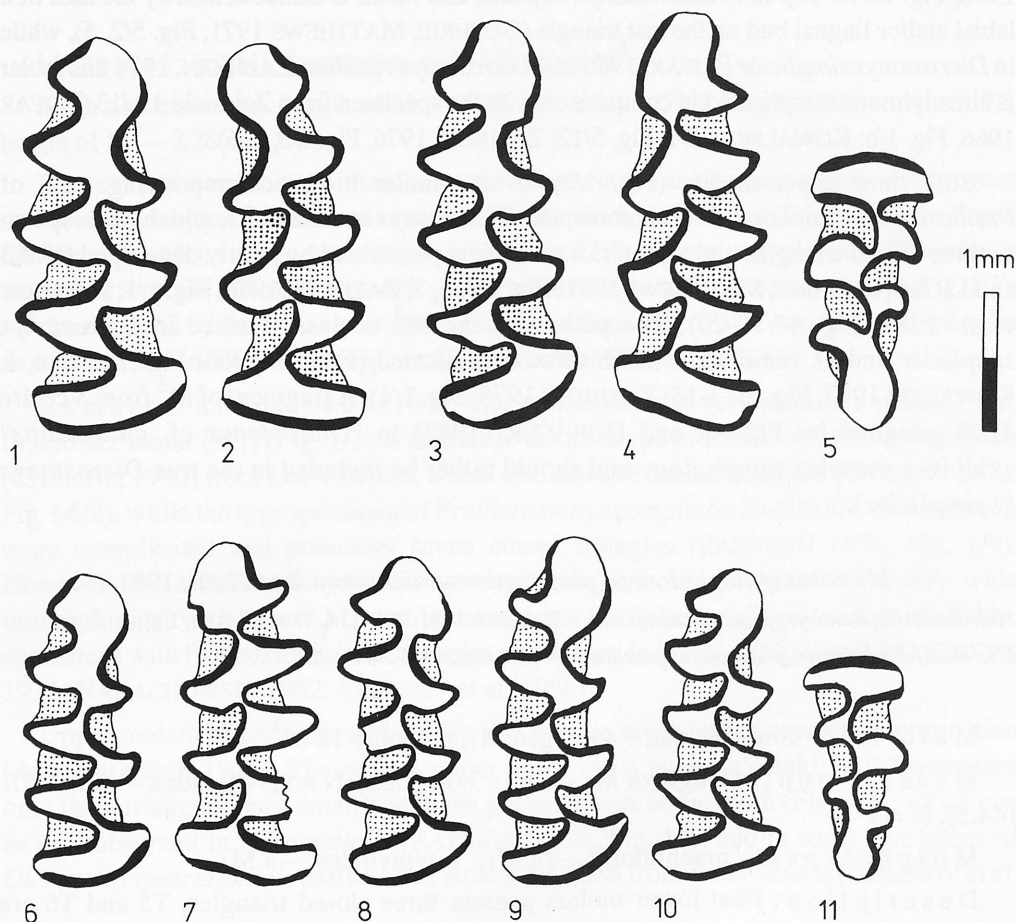


Fig. 2. *Microtus (Allophaiomys) pliocaenicus praehintoni* (1-5) and *Microtus (Allophaiomys) nutiensus* (6-11): 1 – right M_1 , 2 – left M_1 , 3 – right M_1 , 4 – left M_1 , 5 – left M^3 , 6 – right M_1 , 7 – left M_1 , 8 – right M_1 , 9 – right M_1 , 10 – right M_1 , 11 – right M^3 .

Material: 20 complete and 4 damaged M_1 , probably 16 M^3 .

Measurements: length of M_1 – 2.26 – 2.64 (2.47), $N = 20$, A/L index – 42.7 – 49.6 (45.4), $N = 20$

Morphotypes: "praehintoni" – 9 M_1 ; "nutiensus" – 11 M_1 ; "pitymyoides" – 3 M_1 ; "ratticeps" – 1 M_1

Description: Most of the first lower molars are characterized by the confluence of T5 and T6 and development of LRA5 (morphotype "praehintoni" Fig. 2/6) or possess separated T5 and T6, developed BSA4 and a "short" anterior cap (morphotype "nutiensus", Fig. 2/7-8). A few specimens show the separation of T5 and T6, lack of BSA4 and a "high" anterior cap (morphotype "pitymyoides", Fig. 2/9). One specimen possesses four closed

triangles while T5 and T6 are confluent (morphotype "ratticeps", Fig. 2/10). The third upper molars are narrow with two or three closed triangles (Fig. 2/11).

Remarks and discussion: The smaller species of evolved *Microtus* (*Allophaiomys*) is characterized by a very wide variation of M₁. In comparison with the type population of *M. (A.) nutiensis* from Les Valerots (CHALINE 1972), the sample from Zalesiaki 1A/13 is more advanced while the population from Monte Peglia exhibits slightly higher values of the length of M₁ and A/L index (VAN DER MEULEN 1973).

Microtus (Microtus) sp.

Microtus (Microtus) nivaloides – NADACHOWSKI 1990a: Tab. 3

Material: 8 complete and 7 damaged M₁, probably 4 M³

Measurements: length of M₁ – 2.48 - 3.18 (2.78), N = 8, A/L index – 45.3 - 50.4 (47.6), N = 8

Description: first lower molars with separated T4 and T5 and confluent T5 and T6; BSA4 always present; incipient appearance of BRA4 (Fig. 3/1-4); M³ elongated, with LSA5 relatively well developed (Fig. 3/5).

Remarks and discussion: Fossil voles of such a morphological pattern in most cases have been described under the names *Microtus nivaloides* and/or *M. ratticepoides* (e. g. STORCH et al. 1973), although the type populations of these last species from West Runton are distinctly different (NADACHOWSKI 1991). REPENNING (1985) and REPENNING et al. (1990) believe that they belong to the East Asiatic *Lasiopodomys*, which by most neontologists is considered to be a subgenus of *Microtus*. In the opinion of the author they should rather be identified provisionally as *Microtus (Microtus) sp.*

Microtus (Microtus) ex gr. hyperboreus

Material: 3 complete and 3 damaged M₁; probably 3 M³

Measurements: length of M₁ – 2.78 - 2.98 (2.88), N = 2, A/L index – 46.6 - 48.7 (47.6), N = 2

Description: First lower molars characterized by separation of triangles T4, T5 and T6; BSA4 well developed; anterior part of tooth often formed in the shape of a "helmet" (Fig. 3/6-8); third upper molar variable, in most cases with three closed triangles and distinct development of LSA5 (Fig. 3/9-10).

Remarks and discussion: This taxon was recognized in some Early Pleistocene localities in the Russian Plain (e. g. MARKOVA 1982; KRASNENKOV et al. 1984). Further studies are needed to clear the relationship between *M. ex gr. hyperboreus* and *M. (Microtus) sp.* from Zalesiaki 1A. It is probable that they are conspecific.

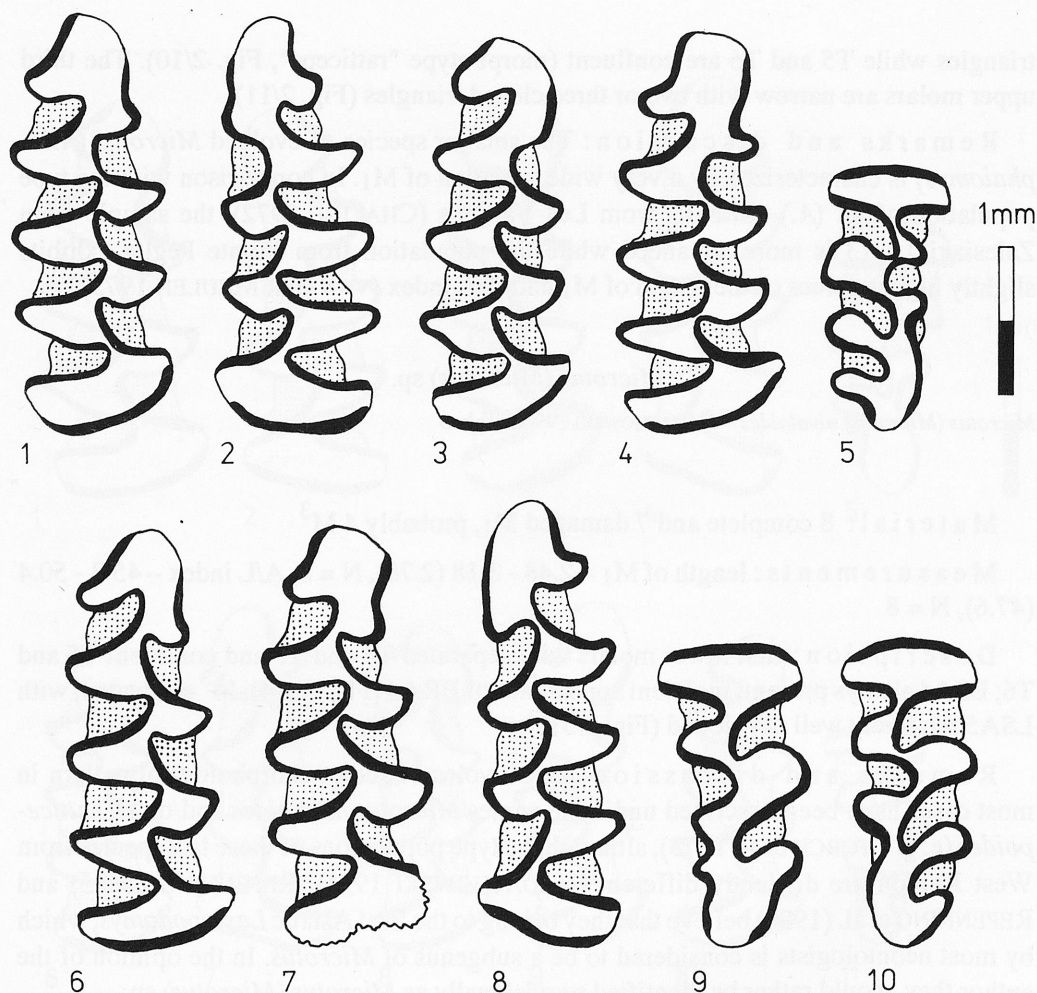


Fig. 3. *Microtus* (*Microtus*) sp. (1-5) and *Microtus* ex gr. *hyperboreus* (6-10): 1 – right M_1 , 2 – left M_1 , 3 – right M_1 , 4 – right M_1 , 5 – left M^3 , 6 – right M_1 , 7 – right M_1 , 8 – left M_1 , 9 – right M^3 , 10 – right M^3 .

IV. FOSSIL RECORD AND EARLY HISTORY OF COLLARED LEMMINGS

In recent years palaeontologists and geologists have come to the conclusion that the part of Beringia situated beyond the Arctic Circle was one of the most important areas of evolution of some characteristic Pleistocene species (HOPKINS et al. 1982). Among rodents, the collared lemmings (*Dicrostonychini*) well exemplify this opinion.

Much attention should be paid to the period lasting from the late Matuyama epoch to early Brunhes (1.5 - 0.5 My), which is considered a major stage of the development of the typical Pleistocene fauna (SHER 1987).

The most primitive collared lemming in Beringia – *Predicrostonyx hopkinsi* – has been found in the Cape Deceit Formation (Alaska) and is believed to be of pre-Cromerian age (GUTHRIE, MATTHEWS 1971) pre-dating or partly coinciding with the Anvilian transgression dated by HOPKINS (1967) between 0.7 and 1.0 My. It is accompanied by *Microtus deceitensis* GUTHRIE et MATTHEWS, 1971 which corresponds morphologically to the evolved *Allophaiomys* in Europe.

Another species, *Predicrostonyx compitalis* has been described from a Chukochya River section, Kolyma Lowland, Northeastern Siberia (ZAZHIGIN 1976) dated to the Early Olyorian (= Chukochyan) (SHER 1987). In this exposure the Early Olyorian is reversely magnetized, containing an episode of normal polarity. This part of the section contains among the small mammal fauna, besides *P. compitalis*, remains of an advanced form of *Microtus* (*Allophaiomys*) *pliocaenicus*. It is also characterized by the absence of true *Microtus* (*Microtus*) and rooted microtines of the genus *Mimomys*. The same association is noted in another important Krestovka River section which is also inversely magnetized. The faunal transition from the Early Olyorian to the Late Olyorian (= Akanian) takes place in the uppermost part of the reversely magnetized zone when the last *Microtus* (*Allophaiomys*) is recorded together with the first *Microtus* (*Microtus*) sp., and *Predicrostonyx compitalis* is replaced by the more evolved *Dicrostonyx renidens*. The latter species of collared lemmings occurs in the Late Olyorian together with several lineages of *Microtus* (*Microtus*) species including *Microtus oeconomus* and *Microtus hyperboreus* – *middendorffi* groups (ZAZHIGIN 1976; SHER et al. 1979; SHER 1987). The foregoing gives ground to date the Olyorian fauna as approximately 1.4-1.2 to 0.6-0.5 million years ago. However, REPENNING (1983, 1984, 1985) placed the Olyorian in the early Matuyama Chron (2.0 - 2.5 My). This interpretation seems to be erroneous according to discussion presented by SHER (1987) which recently has also been accepted by REPENNING (in litt. March, 1991).

Presumably the transition between *Predicrostonyx* and *Dicrostonyx* is represented by the remains listed as "cf. *Dicrostonyx*" by MORLAN (1984) from lower part of Unit 2A at localities 44 and 64 in the Old Crow Basin (Northern Yukon). They are accompanied by "*Microtus* sp. X", which is most similar to *Microtus deceitensis* from the Cape Deceit Formation as well as by some more advanced *Microtus xanthognatus*, *M. cf. miurus* and *M. cf. pennsylvanicus*. This assemblage cannot be univocally interpreted since it contains both Irvingtonian and Rancholabrean elements (MORLAN 1984).

Outside Beringia the Early Pleistocene *Dicrostonychini* have been found in the region of Tobolsk (West Siberia) in the terraces of lower reaches of the Irtysh River (SMIRNOV et al. 1986). The new species described under the name *Dicrostonyx meridionalis* and morphologically very close to *D. renidens*, has been recorded from the localities Skorodum a-c, Romanovo 1c, Romanovo 3 and Krapiva 2. It is associated with *Microtus* (*Allophaiomys*) *pliocaenicus* (advanced form), *Mimomys* ex. gr. *savini*, *Mimomys* cf. *pusillus* and *M. (Cromeromys)* ex. gr. *intermedius*. The Skorodumian faunistic complex is correlated by SMIRNOV et al. (1986) with the Razdolyeian in West Siberia (ZAZHIGIN 1980) and Early Olyorian in Beringia (SHER 1987) and dated by geologists to an interval from 1.0 to 0.76 My (ZUBAKOV, BORZENKOVA 1983).

In Europe probably the oldest remains of collared lemmings from Les Valerots (France), named *Dicrostonyx antiquitatis* (CHALINE 1972), at present included in *Predicrostonyx* (CHALINE 1987), are believed to be of Menapian age (CHALINE et al. 1985). In the assemblage there occurred evolved *Allophaiomys* (CHALINE 1972), most probably represented by two species: the smaller, *Microtus (Allophaiomys) nutiensis*, and the bigger, *Microtus (Allophaiomys) burgondiae*. The latter was lastly referred provisionally to the subgenus *Chionomys* (NADACHOWSKI 1991). The single fragment of M³ from Včeláre 4D/8 referred by FEJFAR and HORÁČEK (1983) to "*Dicrostonyx* cf. *antiquitatis*" had been found in the assemblage containing among rodents *Microtus pitymyoides*, *Pliomys episcopalis* and *Clethrionomys* sp. and thus probably younger than the Les Valerots material. Moreover, the morphological traits of this tooth are advanced representing the typical *Dicrostonyx* (and not *Predicrostonyx*) pattern.

The single tooth of *Dicrostonyx* found together with *Allophaiomys* at Bielle (The Netherlands) above the Tiglian clays (VAN DER MEULEN, ZAGWIJN 1974) is frequently cited as the oldest record of collared lemmings in Europe (REPENNING 1984, 1985; CHALINE 1987; MEAD, MEAD 1989). Taking into account the well documented fossil record from Russia (AGADZHANIAN 1976; ZAZHIGIN 1976; SMIRNOV et al. 1986) this morphologically advanced specimen (*gulielmi* – type) should be considered a contamination from the overlying Pleistocene sediments (SHER 1987).

The systematics of *Dicrostonyxini* is not yet established. It should be noted that GUTHRIE and MATTHEWS (1971), ZAZHIGIN (1976), SHER (1987) and REPENNING (1984, 1985) consider both *Predicrostonyx* and *Dicrostonyx* to be separate genera while FEJFAR and HORÁČEK (1983) include *Predicrostonyx* in the genus *Dicrostonyx*. Moreover, the high polymorphism of dental traits and the phenomenon of the great overlapping of morphological patterns between populations make the taxonomic decisions difficult. Taking into account taxonomically the most important upper molars one can arrange the succession of the Early Pleistocene collared lemming species from most primitive (simple) to most derived (complicated), as follows: *Predicrostonyx hopkinsi*, *P. compitalis*, *Dicrostonyx meridionalis*, *D. renidens* and *D. simplicior*. The European *P. antiquitatis*, which is known exclusively from lower molars should most probably be placed near *P. compitalis*. Traditional nomenclature is kept up in the present paper; however, it is very probable that some of the taxa mentioned are conspecific (e.g. *P. antiquitatis* and *P. compitalis* and/or *D. renidens* and *D. meridionalis*).

V. CONCLUSIONS

Current fossil record of the Early Pleistocene collared lemmings from Palaearctic and Beringia indicates that the oldest remnants of *Dicrostonychini*, assigned here to *Predicrostonyx*, always appear in association with the evolved *Microtus (Allophaiomys)*. Various names were used for the latter in different geographical regions (Table I). It seems, however, that collared lemmings did not occur earlier in the assemblages with typical *M. (Allophaiomys) pliocaenicus* (the record from Brielle is considered to be a contamination). Age control external to faunal interpretation for *Predicrostonyx* indicates a period

Table I.

The most important Early Pleistocene localities with *Dicrostonychini* in Europe, Siberia and Beringia.

Taxon	Locality and geographical region	Accompanying index species	Stratigraphy	Paleomagnetism	References
<i>Predicrostonyx hopkinsi</i>	Cape Deceit, Alaska	<i>Microtus deceitensis</i>	Cape Deceit Formation	?	GUTHRIE, MATTHEWS (1971)
<i>Predicrostonyx compitalis</i>	Chukochya and Krestovka, Northeastern Siberia	<i>Microtus (Allophaiomys) pliocaenius</i> (advanced form)	Early Olyorian (= Chukochyan)	reverse with an episode of normal polarity	SHER et al. (1979), ZAZHIGIN (1976), SHER (1987)
<i>Predicrostonyx compitalis</i>	Zalesiaki 1 A/13, Poland	<i>Microtus (Allophaiomys) pliocaenius praeintoni</i> , <i>M. (A.) nutiensis</i>	Upper Biharian (Q2)	?	this paper
<i>Predicrostonyx antiquitatis</i>	Les Valerots, France	<i>M. (Allophaiomys) nutiensis</i> , <i>M. burgondiae</i>	Menapian	?	CHALINE (1972), CHALINE et al. (1985)
cf. <i>Dicrostonyx</i> sp.	Localities 44 and 64, Old Crow Basin, Northern Yukon	<i>Microtus</i> sp. X <i>M. xanthognathus</i> , <i>M. cf. miurus</i> <i>M. cf. pensylvanicus</i>	Irvingtonian?	?	MORLAN (1984)
<i>Dicrostonyx renidens</i>	Chukochya and Krestovka, Northeastern Siberia	<i>Microtus</i> ex gr. <i>oeconomus</i> <i>Microtus</i> ex gr. <i>hyperboreus</i> - <i>midendorffi</i>	Late Olyorian	reverse (lower part) and normal polarity (upper part)	SHER et al. (1979), ZAZHIGIN (1976), SHER (1987)
<i>Dicrostonyx meridionalis</i>	Skorodum a-c, Romanovo 1-3, Krapiva 2, Irtysh River, West Siberia	<i>Microtus (Allophaiomys) pliocaenius</i> (advanced form)	Skorodumian (= Tobolsk Formation)	?	SMIRNOV et al. (1986)
<i>Dicrostonyx simplicior</i>	Koněprusy C 718, Koněprusy JK 1-2, Czechoslovakia	<i>Minomys savini</i> , <i>Microtus gregoloides</i> , <i>Microtus arvalinus</i>	Upper Biharian (Q2) (Templomegy)	?	FEJFAR (1966)
<i>Dicrostonyx simplicior</i>	Kozi Grzbiet, Poland	<i>Minomys savini</i> , <i>Microtus gregoloides</i> , <i>Microtus</i> ex gr. <i>agrestis</i>	Upper Biharian (Q2) (Templomegy)	normal polarity	KOWALSKI (1977), NADACHOWSKI (1985, 1990a)

ranging from approximately 1.4 ± 0.1 to 0.8 ± 0.1 million years, which corresponds to the upper part of the Matuyama Chron, including the Jaramillo event. *P. hopkinsi* is believed to be an index fossil for the earlier part of this period (before Jaramillo), while morphologically more advanced *P. compitalis* (and probably *P. antiquitatis*) characterize the upper part of the reversed Matuyama Chron. In the late Early Pleistocene, starting approximately from 0.7 ± 0.1 (around the Matuyama / Brunhes boundary) and lasting to 0.5 ± 0.1 My (FAD of *Arvicola*) the collared lemmings are represented by primitive *Dicrostonyx* species (*D. renidens*, *D. meridionalis*, *D. simplicior*). The transition from *Predicrostonyx* to *Dicrostonyx* is probably correlated with the replacement of evolved *Microtus* (*Allophaiomys*) by true *Microtus* (*Microtus*).

REFERENCES

- AGADZHANIAN A. 1976. Die Entwicklung der Lemminge der zentralen und östlichen Paläarktis im Pleistozän. Mitt. Bayer. Staatssamml. Paläont. hist. Geol., **16**: 53-64.
- BANFIELD A. W. F. 1974. The mammals of Canada. University of Toronto Press, 1-438.
- BLACK C. C., KOWALSKI K. 1974. The Pliocene and Pleistocene *Sciuridae* (*Mammalia*, *Rodentia*) from Poland. Acta zool. cracov., **19**(19): 461-484.
- BOURDIER F., CHALINE J., PUISSEGUR J. J. 1969. Données nouvelles sur les Mollusques et les Micromammifères des régions d'Amiens et de Paris. C. R. Acad. Sc., D, **268**: 266-269.
- CHALINE J. 1972. Les rongeurs du Pléistocène Moyen et Supérieur de France. Cahiers de paléont., Paris, 1-410.
- CHALINE J. 1987. Arvicolid data (Arvicolidae, Rodentia) and evolutionary concepts. In: HECHT M. K., WALLACE B., PRANCE G. T. (eds.). Evolutionary biology. Plenum Publ. Corp., **21**: 237-308.
- CHALINE J., RENAULT-MISKOVSKY J., BROCHET G., CLEMENT-DELS R., JAMMOT D., MOURER-CHAUVIRÉ C., BONVALOT J., LANG J., LENEUF N., PASCAL A. 1985. L'aven des Valerots (Nuits-Saint-Georges, Côte-d'Or), site de référence du Pléistocène inférieur. Rev. Geol. Dyn. Geogr. Phys., **26**(2): 109-118.
- CORBET G. B., HILL J. E. 1991. A world list of mammalian species. Third edition. Nat. Hist. Mus. Publ., Oxford University Press, 1-243.
- FEJFAR O. 1965. Die unter-mittelpleistocäne Micromammalier-Fauna aus Dobrkovice, Süd-Böhmen. Ber. geol. Gesell. DDR, **10**(1): 57-65.
- FEJFAR O. 1966. Über zwei neue Säugetiere aus dem Altpleistozän von Böhmen. N. Jb. Geol. Paläont. Mh., **11**: 680-691.
- FEJFAR O. 1976. Plio-Pleistocene mammal sequences. IUGS-UNESCO Internat. Geol. Corr. Progr. Project 73/1/24, Quaternary Glaciations in the Northern Hemisphere. Rep. No. 3, Bellingham (Wash.), **1976**: 251-336.
- FEJFAR O., HEINRICH W.-D. 1983. Arvicoliden-Sukzession und Biostratigraphie des Oberpliozäns und Quartärs in Europa. Schriftenr. geol. Wiss., **19/20**: 61-109.
- FEJFAR O., HORÁČEK I. 1983. Zur Entwicklung der Kleinsäugerfaunen im Villányium und Alt-Biharium auf dem Gebiet der ČSSR. Schriftenr. geol. Wiss., **19/20**: 111-207.
- GRAHAM R. W. 1985. Diversity and community structure of the late Pleistocene mammal fauna of North America. Acta Zool. Fennica, **170**: 181-192.
- GUTHRIE R. D., MATTHEWS J. V. Jr. 1971. The Cape Deceit Fauna - Early Pleistocene mammalian assemblage from the Alaskan Arctic. Quaternary Res., **1**: 474-510.
- HELLER F., BRUNNACKER K. 1966. Halsbandlemming-Reste aus einer oberen Mittelterasse des Rheins bei Niederaussen. Eiszeitalter u. Gegenwart, **17**: 97-112.
- HOPKINS D. M. 1967. Quaternary marine transgressions in Alaska. In: HOPKINS D. M. (ed.). The Bering Land Bridge. Stanford Univ. Press, 451-484.

- HOPKINS D. M., MATTHEWS J. V. Jr., SCHWEGER C. E., YOUNG S. B. (eds.). 1982. Paleoeecology of Beringia. Academic Press, 1-489.
- HORÁČEK I. 1981. Comments on the lithostratigraphic context of the Early Pleistocene biozones of Central Europe. IUGS-UNESCO Internat. Corr. Progr. Preject 73/1/24, Quaternary Glaciations in the Northern Hemisphere. Rep. No. 6, Ostrava, 1979: 99-117.
- HORÁČEK I., SÁNCHEZ MARCO A. 1984. Comments on the Weichselian small mammal assemblages in Czechoslovakia and their stratigraphical interpretation. N. Jb. Geol. Paläont. Mh., 1984(9): 560-576.
- KOWALSKI K. 1977. Fossil lemmings (*Mammalia*, *Rodentia*) from the Pliocene and Early Pleistocene of Poland. Acta zool. cracov., 22(7): 297-317.
- KOWALSKI K. 1979. Fossil *Zapodidae* (*Rodentia*, *Mammalia*) from the Pliocene and Quaternary of Poland. Acta zool. cracov., 23(9): 199-210.
- KOWALSKI K. 1980. Origin of mammals of the Arctic tundra. Folia quatern., 51: 3-16.
- KRASNENKOV R. V., KholmovoI G. V., GLUSHKOV B. V. 1984. Principal sections of the Lower Pleistocene in the upper Don Basin. Voronezh Univ. Press, 1-212. (in Russian)
- LUNDELIUS E. L., GRAHAM R. W., ANDERSON E., GUILDAY J., HOLMAN J. A., STEADMAN D. W., WEBB S. D. 1983. Terrestrial vertebrate faunas. In: H. E. WRIGHT, Jr. (Ed.). Late- Quaternary environments of the United States. Vol. I. The Late Pleistocene. University of Minnesota Press, 311-353.
- MARKOVA A. K. 1982. Pleistocene rodents of the Russian Plain. Nauka, 1-186. (in Russian)
- MEAD E. M., MEAD J. I. 1989. Quaternary zoogeography of the Nearctic *Dicrostonyx* lemmings. Boreas, 18: 323-332.
- MEULEN VAN DER A. J. 1973. Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (*Arvicolidae*, *Rodentia*). Quaternaria, 17: 1-144.
- MEULEN VAN DER A. J., ZAGWIJN W. H. 1974. *Microtus* (*Allophaiomys*) *pliocaenicus* from the Lower Pleistocene near Brielle, The Netherlands. Scripta geol., 21: 1-12.
- MŁYNARSKI M. 1977. New notes on the amphibian and reptilian fauna of the Polish Pliocene and Pleistocene. Acta zool. cracov., 22(2): 13-36.
- MORLAN R. E. 1984. Biostratigraphy and biogeography of Quaternary microtine rodents from Northern Yukon territory, Eastern Beringia. In: GENOWAYS H. H., DAWSON M. R. (eds). Contributions in Quaternary vertebrate paleontology, a volume in memorial to John E. GUILDAY. Special Publ. Carnegie Mus. Nat. Hist., 8: 184-199.
- NADACHOWSKI A. 1982. Late Quaternary rodents of Poland with special reference to morphotype dentition analysis of voles. PWN, 1-108.
- NADACHOWSKI A. 1985. Biharian voles (*Arvicolidae*, *Rodentia*, *Mammalia*) from Kozi Grzbiet (Central Poland). Acta zool. cracov., 29(2): 13-28.
- NADACHOWSKI A. 1989a. Origin and history of the present rodent fauna in Poland based on fossil evidence. Acta theriol., 34(1): 37-53.
- NADACHOWSKI A. 1989b. Gryzonie – *Rodentia*. In KOWALSKI K. (ed.). Historia i ewolucja łądowej fauny Polski. Folia quater., 59-60: 151-176.
- NADACHOWSKI A. 1990a. Lower Pleistocene rodents of Poland: faunal succession and biostratigraphy. Quartärpaläont., 8: 215-223.
- NADACHOWSKI A. 1990b. Review of fossil *Rodentia* from Poland. Senckenbergiana biol., 70(4/6): 229-250.
- NADACHOWSKI A. 1991. Systematics, geographic variation, and evolution of snow voles (*Chionomys*) based on dental characters. Acta theriol., 36(1-2): 1-45.
- NADACHOWSKI A., PAWŁOWSKI J., STWORZEWICZ E. 1989. Charakterystyka stanowisk i ich korelacja stratygraficzna. In: KOWALSKI K. (ed.). Historia i ewolucja łądowej fauny Polski. Folia quatern., 59-60: 5-19.
- PRADEL A. 1988. Fossil hamsters (*Cricetinae*, *Rodentia*) from the Pliocene and Quaternary of Poland. Acta zool. cracov., 31(6): 235-295.

- RABEDER G. 1981. Die Arvicoliden (*Rodentia, Mammalia*) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. Beitr. Paläont. Österr., 8: 1-373.
- REPENNING C. A. 1983. Faunal exchanges between Siberia and North America. Schriftenr. geol. Wiss., 19/20: 333-346.
- REPENNING C. A. 1984. Quaternary rodent biochronology and its correlation with climatic and magnetic stratigraphies. In: MAHANEY W. C. (ed.). Correlation of Quaternary chronologies. Geo Books, 105-119.
- REPENNING C. A. 1985. Pleistocene mammalian faunas: climate and evolution. Acta zool. fenn., 170: 173-176.
- REPENNING C. A., FEJFAR O., HEINRICH W.-D. 1990. Arvicolid rodent biochronology of the Northern Hemisphere. In: FEJFAR O., HEINRICH W.-D. (eds.). International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids, IGCP 216: 385-418.
- SHER A. V. 1987. Olyorian land mammal age of Northeastern Siberia. Palaeontogr. Italica, 74(6): 97-112.
- SHER A. V., KAPLINA T. N., GITERMAN R. E., LOZHKIN A. V., ARKHANGELOV A. A., KISELOV S. V., KOUZNETSOV Yu. V., VIRINA E. I., ZAZHIGIN V. S. 1979. Late Cenozoic of the Kolyma Lowland. XIV Pacific Science Congress. Tour Guide XI, U. S. S. R. Acad. Sci., 1-115.
- SMIRNOV N. G., BOLSHAKOV V. N., BORODIN A. V. 1986. Pleistocene rodents of northern West Siberia. Nauka, 1-145. (in Russian)
- STORCH G., FRANZEN J. L., MALEC F. 1973. Die altpleistozäne Säugetierfauna (*Mammalia*) von Hohensülzen bei Worms. Senckenberg. lethaea, 54(2-4): 311-343.
- YOUNG S. B. 1982. The vegetation of land bridge Beringia. In: HOPKINS D. M., MATTHEWS J. V. Jr., SCHWEGER C. E., YOUNG S. B. (eds.). Paleoeecology of Beringia. Academic Press, 179-191.
- ZAZHIGIN V. S. 1976. Early evolutionary stages of collared lemmings (*Dicrostonychini, Microtinae, Rodentia*) as characteristic representatives of Beringian subarctic fauna. In: Beringia in Cenozoic. U.S.S.R. Acad. Sci., Far-Eastern Scient. Center, 280-288. (in Russian)
- ZAZHIGIN V. S. 1980. Late Pliocene and Anthropogene rodents of the South of Western Siberia. Nauka, 1-156. (in Russian)
- ZUBAKOV V. A., BORZENKOVA I. I. 1983. Paleoclimates of the Late Cenozoic. Gidrometeoizdat, 1-216. (in Russian)